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Linking individual differences in semantic cognition to white matter microstructure

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ABSTRACT

Semantic cognition is thought to involve the interaction of heteromodal conceptual representations with control processes that (i) focus retrieval on currently-relevant information, and (ii) suppress dominant yet irrelevant features and associations. Research suggests that semantic control demands are higher when retrieving a link between weakly-associated word pairs, since there is a mismatch between the pattern of semantic retrieval required by the task and the dominant associations of individual words. In addition, given that heteromodal concepts are thought to reflect the integration of vision, audition, valence and other features, the control demands of semantic tasks should be higher when there is less consistency between these features. In the present study, 62 volunteers completed a semantic decision task, where association strength and semantic-affective congruence were manipulated. We used diffusion tensor magnetic resonance imaging to obtain fractional anisotropy (FA) measures of white matter tracts hypothesized to be part of the semantic network. The behavioural data revealed an interaction between semantic-affective congruence and strength of association, suggesting these manipulations both contribute to semantic control demands. Next we considered how individual differences in these markers of semantic control relate to the microstructure of canonical white matter tracts, complementing previous studies that have largely focused on measures of intrinsic functional connectivity. Repeated-measures analysis of covariance showed opposing interactions between semantic control markers and FA of two tracts: left inferior longitudinal fasciculus (ILF) and right inferior fronto-occipital fasciculus (IFOF). Participants with higher FA in left ILF showed more efficient retrieval of weak associations, and more accurate performance for weak associations when meaning and valence were incongruent, consistent with the hypothesis that this left hemisphere tract supports semantic control. In contrast, participants with higher FA in right IFOF were more accurate for trials in which meaning and valence were congruent, and consequently when semantic control demands were minimised. These findings are consistent with recent studies showing that semantic control processes are strongly left-lateralised. In contrast, long-range connections from vision to semantic regions in the right hemisphere might support relatively automatic patterns of semantic retrieval.

1. Introduction

Our store of conceptual knowledge contains many features and associations, many of which are not relevant at a given moment, and we can flexibly shape retrieval to focus on specific non-dominant properties as required by the circumstances. For example, we know that newspapers are for reading, but when selecting an object to swat a fly, properties such as being rollable and lightweight come to the fore. This capacity for flexible semantic cognition involves the interaction of conceptual representations with control processes (Davey et al., 2016; Jefferies, 2013; Lambon Ralph et al., 2016), and consequently all semantic tasks (including the one used in the current study) are thought to engage these two neurocognitive components (although to varying degrees).

Contemporary theoretical approaches such as the 'Hub and Spokes' model suggest that conceptual representations arise from the integration of multiple types of features, such as visual, auditory, motor, verbal, spatial and emotional, within ventral aspects of the anterior temporal lobes (ATL; e.g., Patterson et al., 2007). Consequently, the same heteromodal conceptual representations – interacting with relevant unimodal

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features ("spokes") – can support the full range of semantic tasks (e.g., Patterson et al., 2007; Lambon Ralph et al., 2016). Recent work has shown that ventral ATL responds to the meaning of words, and not the modality of presentation – i.e., whether these items were spoken or written (Murphy et al., 2017). This structure also responds to the meaningful combination of different features (Coutanche and Thompson-Schill, 2015; Teige et al., 2018) and shows convergence across inputs presented in different modalities, such as verbal and picture-based tasks (e.g., Spitsyna et al., 2006; Visser et al., 2012). Emotional valence can be thought of as a semantic feature (Kousta et al., 2011; Vigliocco et al., 2009), which is integrated in ATL along with vision and audition (Martin, 2016; Olson et al., 2013; Rice et al., 2015a, 2015b; Skipper and Olson, 2014). There is some evidence that emotion is a particularly important feature for the representation of abstract and social concepts in the ATL (Kousta et al., 2011; Vigliocco et al., 2013, 2009). The uncinate fasciculus is thought to play an important role in the integration of meaning and emotion (Bajada et al., 2015a, 2015b; Moritz-Gasser et al., 2015).

Contemporary accounts of semantic cognition suggest these heteromodal semantic representations interact with control processes that shape retrieval (e.g., Lambon Ralph et al., 2016). Semantic control refers to the ability to focus on specific aspects of knowledge, in line with the current context or goal (Whitney et al., 2011). In neuropsychological studies, degradation of heteromodal knowledge following atrophy of the ATL in semantic dementia is qualitatively distinct from deregulated semantic cognition in patients with damage to left hemisphere regions associated with semantic control (Corbett et al., 2009; Jefferies and Lambon Ralph, 2006; Jefferies et al., 2010; Rogers et al., 2015). When semantic retrieval requires dominant aspects of knowledge to be retrieved for a given concept, or a rich concept with multiple coherent features is retrieved, studies have found stronger activation of ATL (Davey et al., 2016; Bemis and Pylkkänen, 2013). Under these circumstances, the requirement for semantic control may be minimised, since semantic retrieval is relatively stable and self-reinforcing. The hypothesized semantic control network may be recruited more strongly when the task requires non-dominant features or associations to be brought to the fore, or to overcome competition between concepts or semantic features. Although early work particularly focussed on the role of left inferior frontal gyrus (IFG) in semantic control, recent studies have demonstrated that a distributed network underpins this function, including posterior middle temporal gyrus (pMTG). Left IFG and pMTG show common activation across a wide range of manipulations of semantic control demands (Noonan et al., 2013) and inhibitory stimulation of both sites disrupts controlled semantic retrieval (Davey et al., 2015a; Whitney et al., 2011). Left IFG and pMTG show strong intrinsic and structural connectivity (Davey et al., 2016). Moreover, damage or inhibitory stimulation to left IFG elicits compensatory increases in pMTG during tasks requiring controlled retrieval (Hallam et al., 2018; Hallam et al., 2016). This semantic control network lies adjacent to, but appears to be partially distinct from, domain-general executive regions (Davey et al., 2016; Noonan et al., 2013).

There has been recent interest in individual differences in semantic cognition, and how these relate to the structure and function of the brain. These studies have examined functional connectivity (Vatansever et al., 2017) and cortical thickness (Wang et al., 2018) but there has been little work relating individual differences in semantic performance to the microstructure of white matter tracts measured with diffusion tensor MRI. Nevertheless, recent studies have improved our understanding of the white matter connections that support semantic cognition. Binney et al. (2012) examined diffusion-weighted imaging within subregions of ATL and found evidence for graded feature convergence, with relative isolation from any given modality within ventral ATL (see also Bajada et al., 2017a, 2017b; Bajada et al., 2015a, 2015b; Fan et al., 2014). In addition, a recent study delineated the possible functional significance of different tracts within the temporal lobe at the group level by linking their termination regions to neuroimaging meta-analytic data (Bajada et al., 2017a, 2017b). In the current study, we examined the association between tract microstructure and individual differences in semantic performance, focusing in particular on behavioural manipulations of semantic control demands.

More than 60 participants completed a previously-used test of semantic control (Marino et al., 2015): they were asked to select the word that was semantically related to a cue word, when the link between the two words was strong (low control) or weaker (high control). Previous research has shown greater involvement of the distributed semantic control network during weak association trials, when it is necessary to shape retrieval to focus on non-dominant aspects of meaning that are currently relevant (Badre et al., 2005; Davey et al., 2015b, 2016; Hallam et al., 2016; Jefferies, 2013; Lambon Ralph et al., 2016; Noonan et al., 2013; Thompson-Schill et al., 1997; Wang et al., 2018; Whitney et al., 2010). In addition, these strong and weak association trials included cues and targets that were either consistent in their emotional valence (i.e., both positive) or inconsistent (i.e., one word was positive, while the other was negative). The demands on semantic control are expected to be maximal in this task when weakly-associated items are also inconsistent in their emotional connotations. Behavioural work has already shown an interaction between semantic association strength and emotional valence congruence (Luna et al., 2016): participants showed less efficient retrieval of weak (non-dominant) associations when emotional valence was also mismatching between the probe and target. More control might be required when the emotional valence is incongruent with the decision, since such pairs of items are thought to have less coherent features within ATL. In these circumstances, there may be some shift in the balance of semantic processing away from ATL and towards the hypothesized semantic control network. To examine the relationship between individual differences on these metrics of semantic control and white matter, we used diffusion tensor magnetic resonance imaging (Basser et al., 1994), assessing the microstructure of semantically-relevant white-matter tracts by computing fractional anisotropy (FA). FA is an index of directionality of diffusion within each voxel and it is associated with integrity of the axonal membrane and thickness of the myelin sheath (Beaulieu, 2002).

We examined four canonical tracts linked to semantic and language processing. The arcuate fasciculus is thought to support the classical dorsal language pathway (Catani and Mesulam, 2008), given it connects comprehension and production areas of language (Catani et al., 2005). The inferior fronto-occipital fasciculus links posterior and inferior frontal regions through the posterior temporal lobe with the occipital lobe (Catani and Thiebaut de Schotten, 2008). Intraoperative electrostimulation as well as lesion studies have shown evidence for this tract being the essential ventral language pathway (Almairac et al., 2015; Duffau et al., 2009), supporting conceptual processing (Kumaran et al., 2009). The role of the inferior longitudinal fasciculus in semantic processes remains unclear (Bajada et al., 2015a, 2015b). This long tract connects the anterior temporal lobe with the occipital lobe (Catani and Thiebaut de Schotten, 2008), and it has been suggested to form part of an indirect ventral language pathway (Mandonnet et al., 2007). The uncinate fasciculus connects the ventral areas of the IFG and orbitofrontal cortex with the temporal pole (Von Der Heide et al., 2013), and has been suggested to contribute to the executive control of semantic processing (Bajada et al., 2015a, 2015b; Binney et al., 2012) as well as the retrieval of valence (Bajada et al., 2015a, 2015b; Moritz-Gasser et al., 2015; Von Der Heide et al., 2013). The dorsal portion of the uncinate fasciculus is a segmentation of special interest, given it arrives at the pars orbitalis and pars triangularis, which are areas that have been associated with semantic control (Badre et al., 2005; Bajada et al., 2017a, 2017b; Noonan et al., 2013). However, the uncinate fasciculus does not terminate in ventral ATL, which is the region thought to be critical for heteromodal semantic representation (Lambon Ralph et al., 2016; Patterson and Lambon Ralph, 2016) – and this tract does not connect to posterior temporal areas also shown to be important for semantic control alongside IFG (Noonan et al., 2013).

2. Methods

2.1. Sample

The sample was composed of 63 Argentinian healthy volunteers aged between 19 and 48 years (M = 27.05, SD = 5.65), of high education level, of which 37 were women. The study protocol was accepted by the Oulton Ethical Committee in accordance with the principles of the Declaration of Helsinki and the participants provided informed consent for their participation in the study.

2.2. Procedure

We adapted a task originally designed by Badre et al. (2005) to measure semantic control (see also Whitney et al., 2011; Whitney et al., 2012). Participants were presented with cue words and were asked to choose the most closely related meaning among three options. Items varied in the strength of association between the cue and target. Weak associations have been shown to activate the semantic control network, along with other task manipulations such as ambiguity and strength of distractors (Noonan et al., 2013). Marino et al. (2015) translated this task into Spanish, matching the words in each condition for concreteness, familiarity and number of letters (see Table 1). There were no significant differences in psycholinguistic properties of the words across the conditions ($p > .05$) (see Table 2).

Marino et al. (2015) also added a manipulation of semantic-affective congruence: the semantically-related options were either congruent in terms of valence (i.e., both positive or both negative) or they were incongruent (one word was positive and the other was negative). In this previous study, there was a bigger effect of congruence for weakly-associated items, suggesting that when controlled semantic retrieval demands are already high, a mismatch in the emotional connotation of words increases control demands further. The words were rated for their affect, control, and arousal, in order to generate semantic-emotional conflicts. The task contained 192 items, with 64 items that were affectively congruent, affectively incongruent, and neutral (no affect).

For establishing the strength of association, we utilized indexes of semantic dictionaries made using the method of free association (Fernandez et al., 2016; Luna et al., 2015). The association strength between cue and target were classified according to the relative frequency of production of the target word following the presentation of the cue word. Strong associations were considered to be those with a relative frequency between 0.50 and 1, and weak associations were those with a relative frequency between 0.02 and 0.05. Half of the items corresponded to strong associations, and half weak, giving rise to six conditions. The task was administered to each participant individually in a single session. A schematic representation of the task is shown in Fig. 1.

2.3. MRI acquisition

All participants were informed of the precautions required for MRI acquisitions. After entering the scanner, 5 min of relaxation and adaptation were given to all participants. The complete MRI acquisition that followed had duration of 22 min.

Images were acquired on a Philips Achieva 1.5 T scanner, using a 12 element SENSE head coil. Thirty-two diffusion weighted and one non diffusion-weighted volume were acquired by eco-planar single-shot imaging, with the following parameters: b-value = 1000 s/mm^2, TR/TE = 9900/80 ms, acquisition and reconstruction matrix size = 112 × 110, FOV = 22.4 × 22 cm, slice thickness = 2 mm, number of slices = 60. In order to correct the DWI for EPI distortions, a structural T1 image was acquired with the following parameters: acquisition and reconstruction matrix size = 240 × 240, TR/TE = 7.05/3.24 ms, FOV = 25.6 × 25.6 cm, number of slices = 249, slice thickness = 1.1 mm, flip angle = 8°.

Table 1
Concreteness, familiarity and letters per item for each condition.[a].

Semantic-affective congruence	Association strength	Concreteness	Familiarity	Letters per item [M (SD)]
Congruent	Strong	4.12 (0.34)	3.93 (0.32)	27.59 (4.34)
	Weak	4.01 (0.32)	3.88 (0.37)	27.78 (3.54)
Incongruent	Strong	4.04 (0.38)	3.89 (0.32)	28.13 (3.54)
	Weak	4.17 (0.35)	4.02 (0.34)	27.91 (4.07)
Neutral	Strong	4.23 (0.37)	4.09 (0.33)	24.25 (3.03)
	Weak	4.21 (0.35)	4.11 (0.30)	24.47 (2.50)

[a] Concreteness and familiarity scores are ratings from 1 to 5.

Table 2
Descriptive statistics of accuracy and RT by condition.

Affect	Association strength	Descriptive statistics			
		Accuracy		RT	
		M	*SD*	*M*	*SD*
Neutral	Strong	.954	.043	1968	353
	Weak	.874	.081	2511	581
Congruent	Strong	.921	.059	2382	444
	Weak	.919	.058	2511	669
Incongruent	Strong	.867	.799	2607	741
	Weak	.814	.112	3143	794

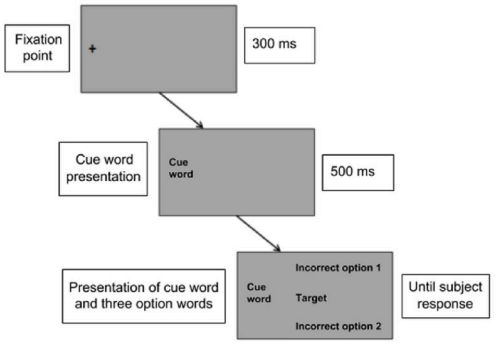
2.4. Image processing

The MR images were processed using MATLAB R2014a and ExploreDTI 4.8.6 (Leemans et al., 2009). First, Gibbs ringing artifacts in the b0 images were corrected with the total variation method (Perrone et al., 2015). Then, subject motion and eddy current induced artifacts were corrected by applying an affine registration of the DWI to the b0 image. The b-matrix was accordingly rotated (Leemans and Jones, 2009). The DWI were non-rigidly registered to the T1 image to correct for distortions due to echo-planar imaging. Finally, the FACT algorithm (Mori et al., 1999) was used to perform whole-brain DTI-based deterministic tractography, with the following parameters: fractional anisotropy threshold for streamline initiation and continuation = 0.2, length threshold 10–500 mm, step size = [2 2 2] mm, angle threshold = 35°.

2.5. DWI analysis

A semi-automated tractography dissection method was applied, previously presented in Lebel et al. (2008). In short, this method requires drawing regions of interest in a reference space to obtain the tracts of interest. The reference space is then registered to the subject's space, and the regions of interest are adapted to obtain the tracts of interest for each subject. In this study, the reference space was an individual case (24 years old woman) randomly selected from the sample.

The methodology for *in-vivo* tractographical dissection by region of interest drawing is thoroughly described in Wakana et al. (2004) and for tract labelling we followed the white matter atlas by Catani and Thiebaut de Schotten (2008). Dissection of the arcuate fasciculus is based on the protocol explained in Lebel and Beaulieu (2009) (see Fig. 2a). The inferior fronto-occipital fasciculus was captured with regions of interest in the frontal and occipital lobes (see Fig. 2b). The inferior longitudinal fasciculus was obtained drawing temporal and occipital regions of interest (see Fig. 2c). The uncinate fasciculus was dissected according to the criteria described in Luna et al. (2016) (see Fig. 2d), with regions of interest in the IFG and the ATL. Segmentation of the dorsal portion of the uncinate fasciculus followed the description by Von Der Heide et al. (2013). All tracts were captured in both hemispheres. We computed average FA for each tract. The use of tract-average microstructural statistics is widespread in the tractography literature (for recent examples, please see: Boukadi et al., 2019; Debarle et al., 2017; Ezzati et al., 2016;



Semantic-affective congruency	Association strength			
	Strong		Weak	
Congruent	VICTORY	YOUTH TRIUMPH BEAUTY	HOME	SHOTGUN FAMILY SCAB
Neutral	INSECT	PAINT BEE STAIR	STEAM	CLOTHING POT BRICK
Incongruent	PARTY	MEADOW ALCOHOL DAWN	DIVORCE	FRAUD RING FEVER

Fig. 1. Schematic representation of the task procedure (left) along with translated examples for each condition of the task (right). The target of each example trial is marked by an arrow.

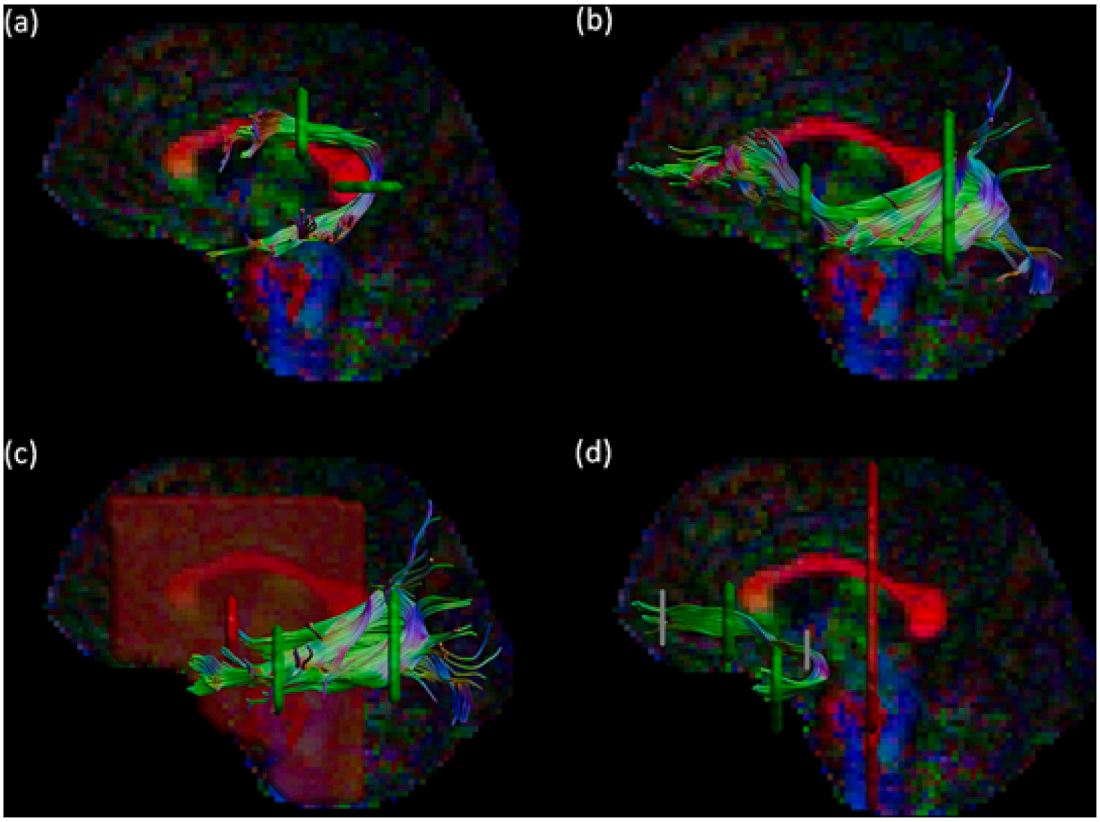


Fig. 2. Dissection through ROI drawing of (a) arcuate, (b) inferior fronto-occipital, (c) inferior longitudinal, (d) and uncinate fasciculus. Inclusive ROIs are displayed in green and exclusive ROIs in red: tracts were selected to pass through the planes shown in green and were excluded if they passed through the planes shown in red. The ROIs used for segmentation of the dorsal portion of the uncinate fasciculus are displayed in grey. First-eigenvector (i.e. principal orientation of diffusion) FA coded colouring is used for visualization of the FA map and the tracts. [color required for print]. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Mole et al., 2016; Smith et al., 2019).

3. Results

3.1. Behavioural task

Our analysis below considers task accuracy, median response time (RT) and response efficiency (RE; computed as RT divided by accuracy), split by condition. Participants with outlying data (±4 standard deviations) in FA or behavioural measures were excluded from the analysis (N = 1). Reaction time was not significantly correlated with accuracy ($r = 0.243$, $p = .058$), although there was a correlation with reaction time variability (calculated as the subject's coefficient of variation in reaction time; $r = 0.383$, $p = .002$).

The effects of semantic-affective congruence, association strength and their interaction on accuracy, RT and RE are shown in Fig. 3. For neutral affect trials, there was a significant accuracy difference between strong and weak associations ($t = 8.077$, $p < .001$). The same pattern was observed for RT ($t = 10.569$, $p < .001$) and RE ($t = 12.400$, $p < .001$). Our previous studies (Luna et al., 2016; Marino et al., 2015) have also shown significant interactions between strength of association and emotional congruence. This effect was replicated in these data using repeated measures ANOVA (see Table 3). For accuracy, there were significant main effects of semantic-affective congruence, strength of

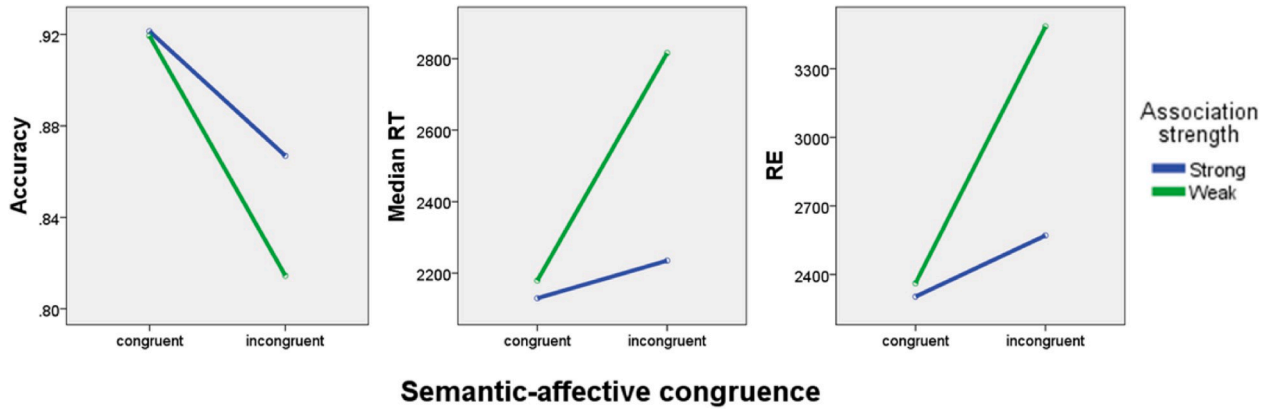


Fig. 3. Interactions between semantic-affective congruence and association strength for accuracy, median RT and RE. [color required for print]. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

association, and an interaction between these factors, reflecting a significant effect of strength of association for the incongruent trials ($p < .001$) but not for the congruent condition ($p = .738$). Repeated measures ANOVA examining RT and RE identified similar effects (see Table 3). Post-hoc analysis for the RT and RE interactions also showed a significant effect of strength of association for incongruent (RT: $p = .006$; RE: $p < .001$) but not for congruent trials (RT: $p = .185$; RE: $p = .153$).

3.2. Behavioural effects and white matter microstructure

Next, we investigated the relationship between individual differences in FA of white matter pathways that might contribute to semantic control and the effects of associative strength and emotional congruence.

To that end, we conducted repeated measures ANCOVAs, with two factors (emotional congruence, and association strength between cue and target). We standardized accuracy, RT and RE values in the four task conditions, as well as FA values of all the segmented tracts. A complete factorial model was defined for each dependent measure, with all FA measures being included simultaneously in each model (see Tables 4–6). Significant associations between behaviour and FA that can survive Bonferroni correction for the three models are highlighted in these tables below.

To explore the underlying pattern of these significant interactions, we plotted the differences in performance between conditions that were associated with individual differences in FA (see Figs. 4 and 5).

Fig. 4 shows that the relationship between FA of the left inferior longitudinal fasciculus and the effect of associative strength on semantic performance varied as a function of semantic-affective congruence. In the semantic-affective congruent condition, those participants with higher FA for the left inferior longitudinal fasciculus performed relatively well on strong association trials. In the semantic-affective incongruent condition, this difference was reduced or reversed: participants with higher FA within the left inferior longitudinal fasciculus were relatively good at weak associations.

In Fig. 5, it can be seen that participants who were relatively good at semantic-affective congruent trials had higher FA in the inferior fronto-occipital fasciculus of the right hemisphere, and those who were relatively good at incongruent trials had lower FA.

Two further repeated measures ANCOVAs, focusing on median RT and response efficiency (see Tables 5 and 6) found an association between FA in left inferior longitudinal fasciculus and the effect of strength of association. In Fig. 6, it can be seen that participants who were relatively good at retrieving weak associations showed higher FA in the left inferior longitudinal fasciculus.

Table 3
Behavioural effects on accuracy, median RT and RE.

Performance measure	*Semantic-affective congruence*		*Association strength*		*Semantic-affective congruence * association strength*	
	F	*η2*	*F*	*η2*	*F*	*η2*
Accuracy	115.662	0.655	20.209	0.249	15.12	0.199
Median RT	111.735	0.647	100.918	0.623	84.339	0.58
RE	133.902	0.687	120.441	0.664	84.743	0.581

$p < .001$ for all behavioural effects. RT = response time. RE = response efficiency (RT/accuracy). This score was not inverted; larger scores corresponded to weaker performance.

4. Discussion

We found that individual differences in the microstructure of white-matter tracts relate to between-participant variation in the ability to shape semantic retrieval to suit the context. Previous research using similar task contrasts of weak and strong semantic associations found dissociations between (i) brain regions implicated in long-term semantic storage and (ii) areas that are engaged when non-dominant aspects of knowledge are needed or when different semantic features are inconsistent (Badre et al., 2005; Davey et al., 2015b; Hallam et al., 2016; Jefferies, 2013; Lambon Ralph et al., 2016; Noonan et al., 2013; Whitney et al., 2010). In these circumstances, relatively automatic patterns of semantic retrieval, which can efficiently recover dominant aspects of knowledge, are unlikely to be sufficient for successful semantic cognition (Jefferies, 2013; Lambon Ralph et al., 2016) (although we acknowledge that all semantic tasks involve a combination of conceptual representations and control processes, and that task contrasts are not process-pure). Higher FA within the right inferior fronto-occipital fasciculus was associated with a stronger effect of semantic-affective congruence (i.e. fewer errors on emotionally congruent trials). FA for this right-hemisphere tract was therefore linked with better performance on potentially less controlled semantic decisions, in which emotional valence and semantic similarity were not in conflict. In contrast, FA of the left inferior longitudinal fasciculus was associated with better performance on semantic decisions requiring greater control – in particular, the efficient retrieval of weak associations, and more accurate performance on weak associations when emotional valence was incongruent with meaning. While access to weak associations also requires conceptual representations, it is notable that the same left-lateralised tract was associated with both task manipulations thought to be relevant to semantic control. The left inferior longitudinal fasciculus may therefore be relevant to the functions of the semantic control network.

Table 4
Interactions between repeated measures effects on accuracy and FA of the segmented tracts.

Fasciculus	Hemisphere	*Semantic-affective congruence*			*Association strength*			*Semantic-affective congruence * association strength*		
		F	p [a]	η2	F	p [a]	η2	F	p [a]	η2
Arcuate	R	0.981	.327	.019	0.494	.485	.010	1.050	.310	.020
	L	0.394	.533	.008	2.743	.104	.051	1.922	.172	.036
Inferior longitudinal	R	1.266	.266	.024	0.037	.849	.001	1.250	.269	.024
	L	0.000	.997	.000	2.624	.111	.049	5.592	**.022**	.099
Inferior fronto-occipital	R	6.512	**.014****	.113	0.011	.918	.000	0.951	.334	.018
	L	1.179	.283	.023	1.982	.165	.037	0.164	.687	.003
Uncinate	R	0.052	.821	.001	2.176	.146	.041	1.622	.209	.031
	L	1.053	.310	.020	0.096	.758	.002	0.029	.866	.001
Dorsal uncinate	R	0.092	.763	.002	0.188	.667	.004	0.090	.765	.002
	L	0.187	.667	.004	0.097	.757	.002	0.804	.374	.016

[a] p-values below .05 are highlighted. The p values are uncorrected but results that survive Bonferroni correction for the use of three models (examining accuracy, RT and RE) are marked with **.

Table 5
Interactions between repeated measures effects on median RT and FA of the segmented tracts.

Fasciculus	Hemisphere	*Semantic-affective congruence*			*Association strength*			*Semantic-affective congruence * association strength*		
		F	p [a]	η2	F	p [a]	η2	F	p [a]	η2
Arcuate	R	0.312	.579	.006	0.008	.928	.000	1.052	.310	.020
	L	0.002	.968	.000	0.908	.345	.018	0.817	.370	.016
Inferior longitudinal	R	1.605	.211	.031	3.334	.074	.061	0.000	.989	.000
	L	0.403	.529	.008	4.509	**.039**	.081	0.024	.878	.000
Inferior fronto-occipital	R	1.775	.189	.034	0.624	.433	.012	0.653	.423	.013
	L	0.296	.589	.006	0.019	.892	.000	0.087	.769	.002
Uncinate	R	2.415	.126	.045	2.836	.098	.053	0.616	.436	.012
	L	0.229	.634	.004	0.58	.450	.011	2.007	.163	.038
Dorsal uncinate	R	0.628	.432	.012	0.183	.670	.004	0.256	.615	.005
	L	0.356	.553	.007	0.400	.530	.008	1.591	.213	.030

[a] p-values below .05 are highlighted. The p values are uncorrected for the use of three models (examining accuracy, RT and RE).

Table 6
Interactions between repeated measures effects on response efficiency and FA of the segmented tracts.

Fasciculus	Hemisphere	Semantic-affective congruence			Association strength			Semantic-affective congruence * association strength		
		F	p [a]	η2	F	p [a]	η2	F	p [a]	η2
Arcuate	R	1.070	.306	.021	0.025	.875	.000	2.158	.148	.041
	L	0.053	.818	.001	1.666	.203	.032	0.015	.901	.000
Inferior longitudinal	R	3.468	.068	.064	0.007	.932	.000	0.316	.576	.006
	L	0.000	.995	.000	7.338	**.009****	.126	1.746	.192	.033
Inferior fronto-occipital	R	2.308	.135	.043	0.005	.942	.000	0.905	.346	.017
	L	0.019	.892	.000	0.424	.518	.008	0.019	.891	.000
Uncinate	R	1.691	.199	.032	0.919	.342	.018	0.075	.786	.001
	L	0.946	.335	.018	0.338	.564	.007	0.605	.440	.012
Dorsal uncinate	R	0.317	.576	.006	0.001	.981	.000	0.02	.889	.000
	L	0.735	.395	.014	0.164	.687	.003	1.224	.274	.023

[a] p-values below .05 are highlighted. The p values are uncorrected but results that survive Bonferroni correction for the use of three models (examining accuracy, RT and RE) are marked with **.

The inferior fronto-occipital fasciculus is associated with basic language processes such as reading (Catani and Thiebaut de Schotten, 2008). Anatomically, this is a long range tract that carries information anteriorly from medial occipital and temporal lobes (Kumaran et al., 2009). This tract goes through temporal and occipital regions, reaching the ATL via the medial temporal lobes. This anatomical localization suggests this tract may play a critical role in delivering information from visual 'spoke' regions to the heteromodal hub in ventral ATL. The inferior longitudinal fasciculus is also a ventral association tract that connects the occipital and temporal lobes, reaching the anterior temporal lobe. It has been shown to be involved in visual perception and memory, facial recognition, and language functions (Catani and Thiebaut de Schotten, 2008; Hodgetts et al., 2017; Panesar et al., 2018). Both of these tracts potentially play a critical role in supporting interactions between visual 'spoke' regions and heteromodal conceptual representations in ATL (Bajada et al., 2017a, 2017b). However, tracts in the left hemisphere are likely to play a more important role in semantic control, which is strongly left-lateralised (Gonzalez Alam et al., 2018; Noonan et al., 2013), potentially accounting for the different behavioural associations we observed in the current study. Gonzalez Alam et al. (2019) recently characterised the lateralisation of different semantic sites in resting-state fMRI data. The intrinsic connectivity between key regions implicated in semantic control (IFG; pMTG) was found to be stronger in the left hemisphere, suggesting these sites form a left-lateralised functional network recruited when we shape semantic processing to suit the circumstances. In contrast, ATL implicated in semantic representation has more symmetrical connectivity (Gonzalez Alam et al., 2018), consistent with studies suggesting that the conceptual store is bilateral (Jung and Lambon Ralph, 2016; Pobric et al., 2010; Rice et al., 2015a, 2015b).

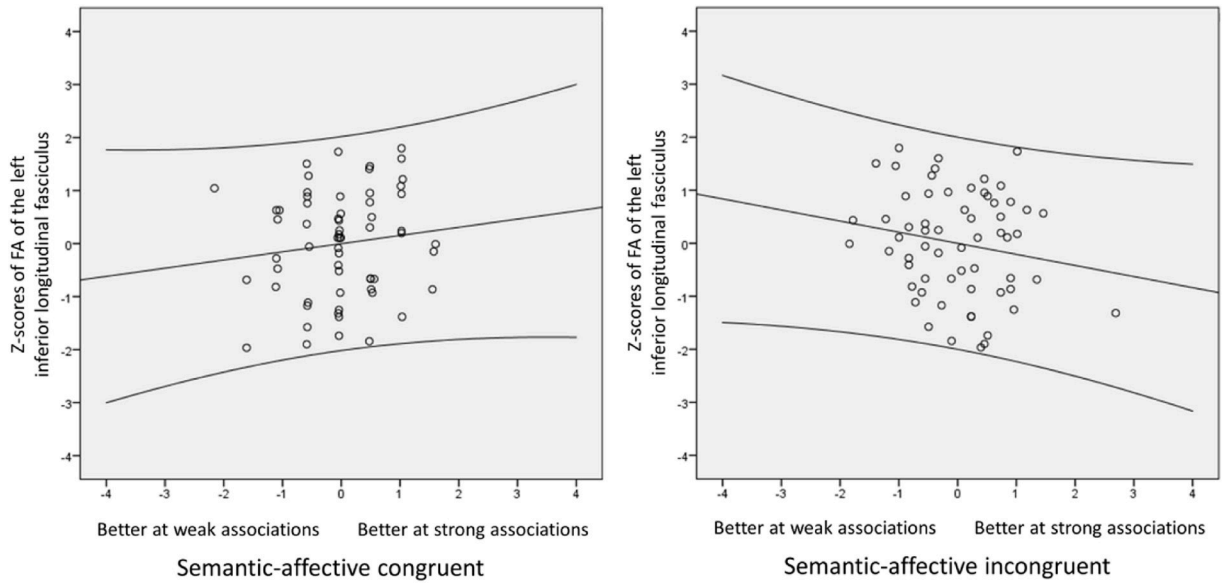

Z-scores of FA of the left inferior longitudinal fasciculus
Better at weak associations
Better at strong associations
Semantic-affective congruent
Z-scores of FA of the left inferior longitudinal fasciculus
Better at weak associations
Better at strong associations
Semantic-affective incongruent

Fig. 4. Scatter plot of between-conditions z-scores differences of performance on each semantic-affective condition and z-score of FA of the left inferior longitudinal fasciculus. The black lines represent the linear fit and the between-subjects 95% confidence interval.

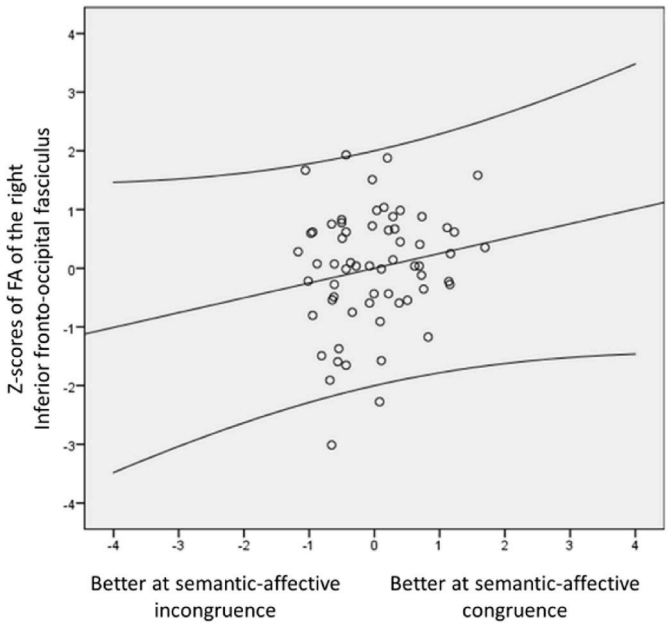

Z-scores of FA of the right Inferior fronto-occipital fasciculus
Better at semantic-affective incongruence
Better at semantic-affective congruence

Fig. 5. Scatter plot of differences in z-score of performance between semantic-affective conditions and z-score of FA of the right inferior fronto-occipital fasciculus. The black lines represent the linear fit and the between subjects 95% confidence interval.

Previous studies have examined the functions of these two occipital-temporal tracts in semantic and language tasks. Our findings are broadly consistent with the findings of Nugiel et al. (2016), who found an association between the integrity of both left inferior fronto-occipital and inferior longitudinal fasciculus in semantic retrieval, using a verb generation task in a sample of 36 participants. In general terms, both studies link white matter lateralisation to semantic control demands, with right hemisphere tracts implicated in performance in low-demand conditions and left hemisphere tracts in high-demand conditions. We have provided converging evidence that left and right-sided tracts are associated with distinct aspects of semantic retrieval, in a larger sample, using a different task and applying established methods to correct for imaging artifacts such as Gibbs ringing (Perrone et al., 2015) and eco-planar imaging induced distortions (Irfanoglu et al., 2013). However, the different behavioural associations to these tracts – with right IFOF implicated when emotional valence and semantic similarity were not in conflict and left ILF implicated when weak associations were efficiently retrieved – suggests IFOF and ILF may also show some functional dissociations (Almairac et al., 2015; Duffau, 2015; Mandonnet et al., 2007). Mandonnet et al. (2007) used direct electrical stimulation during surgery to assess the role of the left inferior longitudinal fasciculus and inferior fronto-occipital fasciculus in language. While stimulation of the inferior fronto-occipital fasciculus provoked semantic paraphasias in several patients, no basic disturbance was observed when stimulating the inferior longitudinal fasciculus. A similar pattern was found by Almairac et al. (2015), who evaluated verbal fluency tasks in patients following surgery for left diffuse low-grade glioma: the volume of infiltration in the fibres corresponding to the inferior fronto-occipital fasciculus was negatively correlated with verbal fluency scores, while this effect was not observed for the inferior longitudinal fasciculus. These studies are consistent with the view that the inferior fronto-occipital fasciculus is an essential tract of the ventral stream supporting conceptual access, while a role for left inferior longitudinal fasciculus might only emerge when high-control semantic tasks are contrasted with low-control conditions.

The main methodological limitation of this study is that diffusion tensor imaging cannot represent multiple differently oriented fiber populations in a single voxel (Jeurissen et al., 2013). Thus, in regions where fibers cross, branch or kiss, tensor-derived measures such as FA are unreliable. Nevertheless, this study shows that white matter in both hemispheres is associated with individual differences in semantic cognition, but in opposing ways. Right IFOF might support more 'automatic' patterns of semantic retrieval, when valence is congruent with meaning and consequently there is no conflict. In contrast, left ILF is associated with more controlled patterns of semantic retrieval, consistent with the left-lateralised network for semantic control which implicates left pMTG alongside left IFG. For example, left ILF might play an important role in allowing left pMTG – a key region implicated in semantic control – to shape ongoing semantic retrieval within ATL, and/or to gate interactions between ATL and vision to promote relevant information.

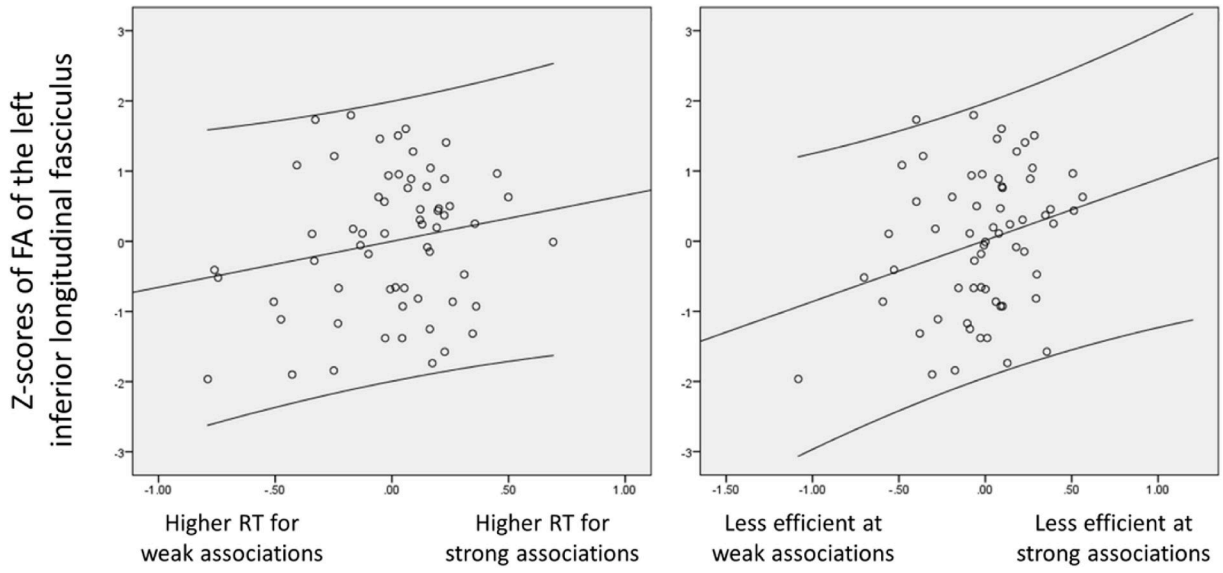

Z-scores of FA of the left inferior longitudinal fasciculus
Higher RT for weak associations
Higher RT for strong associations
Less efficient at weak associations
Less efficient at strong associations

Fig. 6. Scatter plot of differences in z-score of performance between semantic-affective conditions and z-score of FA of the left inferior longitudinal fasciculus. The black lines represent the linear fit and the between subjects 95% confidence interval.

CRediT authorship contribution statement

Julián Marino Dávolos: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Juan Cruz Arias:** Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Elizabeth Jefferies:** Conceptualization, Writing - original draft, Writing - review & editing, Visualization.

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